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A South East Asian ponerine ant of the genus *Leptogenys* (Hym., Form.) with army ant life habits*

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Summary. The emigration and raiding behavior of the SE Asian ponerine ant *Leptogenys* sp. 1, which resembles *L. mutabilis*, were observed in the field (Ulu Gombak, Malaysia). The ants formed monogynous colonies that consisted of up to 52100 workers. The bivouac sites of this species were found in leaf litter, rotten logs, ground cavities, etc., and were rarely modified by the ants. The colonies stayed in these temporary nests for several hours to 10 days; afterwards, they moved to a new nest site. The emigration distances ranged from 5–58 m. Since nest changing takes place at irregular intervals, and pupae and larvae are always present in the nest relocations of *Leptogenys* sp. 1, the emigration behavior is not linked to a synchronized brood development. *Leptogenys* sp. 1 is a nocturnal forager; in our study, up to 42600 workers participated in each raid. The ants move forward on a broad front; behind the swarm a fan-shaped network of foraging columns converges to form a main trunk trail. A new system of foraging trails is developed in each raid. The workers search for their prey collectively; they attack and retrieve the booty together. The diet of *Leptogenys* sp. 1 consists mainly of arthropods. Army ant behavior is characterized by (1) formation of large monogynous colonies, (2) frequent emigrations, and (3) mass raids in which all foraging activities are carried out collectively. Since *Leptogenys* sp. 1 performs these typical army ant behavior patterns, this species represents the army ant ecotype. However, this species differs considerably from army ant species that have synchronized broods and huge colonies with dichthadiiform queens.

Introduction

In the tropics of Africa and America, army ants of the subfamilies Dorylinae and Ecitoninae are faunal elements of outstanding ecological importance. They perform impressive mass raids and colony movements. Most conspicuous are the swarm-raiding epigaeic prey generalists, e.g., *Dorylus (Anomma) wilverthi* in Africa (Raignier and van Boven 1955) and *Eciton burchelli* and *Labidus praedator* in the neotropical region (Rettenmeyer 1963; Schneirla 1971).

Doryline ant species occur also in SE Asia, but the *Dorylus* species of this region are subterranean foragers, and *Aenictus* species prey mainly on various ant species (Wilson 1964). Swarm raiding epigaeic *Dorylus* species are not found in SE Asia. Gotwald (1979) hypothesized that the lack of diversity in this genus in Asia might be due to competitive exclusion by other ant species with army ant life habits that were already well established when *Dorylus* dispersed to this zoogeographical region. This idea is supported by investigations on *Aenictus gracilis* and *Aenictus laeviceps* in the Philippines (Schneirla and Reyes 1966). These species prey on a broader range of invertebrates and show transitions to swarm raiding behavior. Moffett (1984) described swarm raiding behavior also in the myrmicine ant *Pheidologeton diversus*.

During our research on migrating ants in the tropical rain forest of the Malayan Peninsula, we observed a ponerine ant species that performs spectacular mass raids and nest relocations. Here we report that this ant species indeed represents the army ant ecotype and resembles the Dorylinae and Ecitoninae in many aspects of its life history. Specimens of the species were sent for identification to B. Bolton, British Museum (Natural History), London. The species belongs to the *Leptogenys*

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* Dedicated to Professor Dr. M. Lindauer on the occasion of his 70th birthday

Offprint requests to: U. Maschwitz

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Table 1. Emigrations of *Leptogenys* sp. 1, Colony 1, during a 7 week period: start, duration, and distance of colony movements, and the location of the new bivouac. Three short range site shifts (<3 m) along the rotten log were observed between nights 13–23

Night	Into bivouac No	Stay at bivouac (days)	Start (h)	Duration (min)	Distance (m)	Nest site
1	1	3	0300	?	?	leaf litter
4	2	1	0320	161	49	ground cavity
5	3	5	2230	230	6	leaf litter
10	4	3	0310	170	30	ground cavity
13	5	10	0100	167	38	rotten log
23	6	4	2150	213	11	rotten log
27	7	4	2010	159	24	leaf litter
31	8	6	0020	165	19	rotten log
37	9	0	0335	153	58	leaf litter
	10	2	0500	?	9	ground cavity
39	11	0	2000	?	22	leaf litter
	12	1	0020	173	27	leaf litter
40	13	0	2220	124	15	leaf litter
	14	1	0320	175	5	ground cavity
41	15	1	0230	171	19	leaf litter
42	16	1	2110	170	11	rotten log
43	17	1	?	?	5	rotten log
44	18	3	0300	?	29	ground cavity
47	19	?	0330	?	?	ground cavity
		$n=18$ $\bar{x}=1.5$		$n=12$ $\bar{x}=166$	$n=17$ $\bar{x}=19$	

Frequency of colony emigrations. From the beginning of our observations in 1973, we found that the colonies usually left their nesting sites within 1 to 3 days. This indicates a frequent relocation of nesting sites. For 7 weeks we observed the emigration behavior of one colony of *Leptogenys* sp. 1. During this period, the whole colony moved 19 times over longer distances (>3 m). The colony stayed in one site up to 10 days ($\bar{x}=1.5$ days, $n=18$). During the 10-day stay, the ants shifted their nesting site three times over short distances (<3 m). However, in the 37th, 39th and 40th night, the ants abandoned their new bivouac already after a few hours. In each of these nights, therefore, we observed two emigrations. More details are given in Table 1.

Distances and directions of colony emigrations. In Fig. 6 a map of the movements of this colony during the 7 weeks is given. The distance covered by a single emigration varied from 5 to 58.7 m ($\bar{x}=19$ m, $n=17$). The statistical analysis (Raleigh-test, Batschelet 1981) of the directions of the emigrations shows that the choice of a new nest site is not made at random. The direction from the old to the new site deviated 28° on average from the direction chosen in the previous emigration, even if the 90° turns (bivouacs 2, 15, 18), which were obviously induced by hitting an obstacle (stream, road, forest border), are included ($r=0.70$, $n=17$, $P<0.001$).

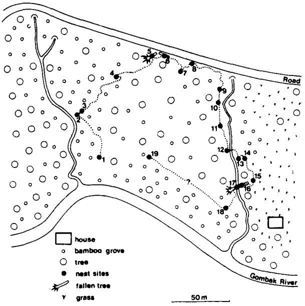

Fig. 6. Nest relocations of a colony of *Leptogenys* sp. 1 during an observation period of 49 nights

Guests

Like the colonies of Dorylinae and Ecitoninae, *Leptogenys* sp. 1 was accompanied by a large

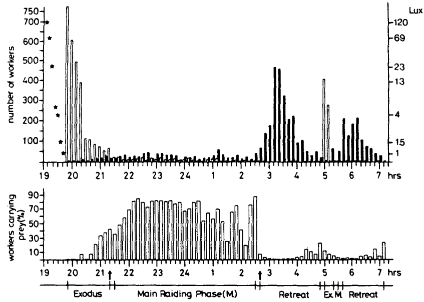

Fig. 7. Ant traffic on the main trail close to the nest entrance (night 17); above: □ workers leaving the bivouac within 1 min; ■ workers returning to the bivouac within 1 min; ★ light intensity; below: □ rate of prey-laden workers

number of guests. Their number varied from colony to colony. Many species of guests followed the emigration trail during or shortly after the nest relocation. We observed at least two species of staphilinid beetles (see Note added in proof); a lepismatid, which was sometimes transported on pupae; a reddish spider (Oonopidae); white collembolans; and females of the recently described phorid species *Puliciphora rosei,* which was observed to be associated with *Leptogenys mutabilis* (Disney 1988) and a hitherho undescribed species of *Rhynchomicropteron.*

Several guest species are carried on different stages of the brood apparently depending on their special residence site in the colony. *Exalloniscus maschwitzi,* an isopod species that is greatly adapted to its myrmecophilous life (Ferrara et al. 1987), often clings to the end of a pupa and is thereby carried to the new bivouac. We observed up to four individuals of a tiny ptiliid beetle on top of a pupa and also observed mites riding on pupae. On the larvae we found a larger dark ptiliid beetle, a whitish beetle with partly reduced wings, and several mites. A mite species was also observed on the workers.

Foraging behavior

Leptogenys sp. 1 forages nocturnally. The raids began at dusk and ended before or shortly after dawn. During the observation period, 1–3 raids per night ($\bar{x} = 2$, $n = 7$) were conducted. In every raid a new trail system was developed (Fig. 8). We registered up to 38,400 participants in each raid (16,700–38,400, $\bar{x} = 27{,}200$, $n = 11$). Three raid phases were distinguished: the exodus, the main raiding phase, and the retreat (Fig. 7).

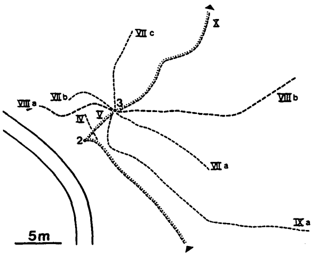

Fig. 8. Raid courses conducted from bivouacs 2 and 3 (no measurings were taken on nights 6 and 9, and after the nest relocations on nights 4 and 5). (— — — raid trail; ···· emigration trail)

Exodus. The forays started after sunset between 1920 and 1945 hours. The first activities that could be seen outside the bivouac were groups or columns of workers moving beneath the leaves. From there they expanded rapidly in several directions into the leaf litter around the bivouac. They advanced by forming pseudopodia-like formations, which consisted of hundreds of workers, or narrow columns. The main trail on which the mass exodus occurred was established within 20–60 min ($n = 5$). During the exodus, the outgoing traffic dominated

Table 2. *Leptogenys* sp. 1. Number and duration of raids. Average rate of returning prey-laden workers (observation period: 11 nights)

Night	Number of raids	Raiding time	Duration (min)	Exodus (min)	Main raiding phase (min)	Retreat (min)	Rate of returning laden ants
4	>1	a) 1920–0310	480	130	260	090	39.0%
5	>2	a) 1940–2220	170	090	–	080	–
		b) 2045–2220	105	085	020	–	31.5%
8	2	a) 1935–0400	475	105	200[a]	170	54.4%
		b) 0245–0710	265	075	100	090	37.1%
9	1	1930–0620	660	200	330	130	62.2%
10	>1	a) 1930–0300	460	090	250	120	44.1%
12	1	1940–0320	?	220[a]	130	110[a]	57.4%
13	>1	a) 1945–0050	315	115	170	030	48.1%
14	2	a) 1945–0110	335	115	090	130	32.8%
		b) 0030–0720	415	070	255	090	49.2%
17	2	a) 1940–0500	570	110	310	150	71.1%
		b) 0500–0710	150	030	010	100	04.0%
18	2	a) 1930–2120	130	040	010	070	02.0%
		b) 2100–0720	630	080	400	150	62.1%
19	3	a) 1930–0020	300	110	100	090	66.0%
		b) 0000–0220	150	070	080	–	36.3%
		c) 0230–0850	390	030	230	130	56.2%
	$n=7$ $\tilde{x}=2$		$n=17$ $\tilde{x}=320$	$n=18$ $\tilde{x}=90$	$n=17$ $\tilde{x}=170$	$n=16$ $\tilde{x}=100$	$n=17$ $\tilde{x}=48.1\%$

[a] Delay or total interruption of raiding activities by heavy rainfalls

the principal trail. Increasing numbers of workers left the bivouac; at the height of the exodus, sometimes more than 1000 workers per min, i.e., up to 13 rows abreast, travelled at the base of the trunk trail. A few workers walked in the opposite direction towards the bivouac dragging their gasters over the ground, presumably laying pheromone trails. We regarded an exodus as completed when in two successive measurings less than 50 workers per min were recorded leaving the bivouac.

Main raiding phase. The foray reached its height during the main raiding phase, which varied in length from a few minutes to several hours (10–400 min, $\tilde{x}=170$ min, $n=17$). During the main raiding phase, there was low level traffic on the trunk trail in both directions, whereas many thousands of foragers were involved in the big swarm raid. Up to 88% of the returning ants were carrying prey to the bivouac. More details are given in Table 2 and Fig. 9.

Retreat. The period of balanced traffic to and from the bivouac was followed by the retreat, which continued for 30–150 min ($\tilde{x}=105$ min, $n=16$). When the homebound traffic started to prevail (> 50 workers per min), the percentage of burdened workers rapidly decreased to less than 10%. We observed the beginning of the retreat as a nearly synchronous turn of the ants at the forefront of the swarm. The wave of return moved along the fan of columns behind the swarm and finally reached the bivouac. Outgoing ants turned after frequent collisons with nestmates that were returning to the nest; nevertheless, there were still some workers leaving the nest entrance until the end of the foray. Frequently, a new exodus or an emigration already began while the last workers from the previous raid were still returning to the bivouac.

Swarm raid. In the "amoeba-like" structure that was formed by the workers spreading out from the bivouac after sunset, one of the "pseudopodia" became very attractive. The ants accumulated at this point and, as the mass advanced, the swarm became an organized unit. The workers at the forefront explored the area by slowly moving about and palpating the substrate, investigating leaf litter, subterranean cavities, and rotten logs. They also ascended the vegetation up to 5 m. As the swarm moved forward, a fan-shaped network of columns developed behind it. The trail system converged in the back forming a main trunk trail that permanently connected the swarm to the temporary nest (Fig. 9). Narrow columns developed at the flanks of the swarm and in the direction of its advance.

Table 3. *Leptogenys* sp. 1. Size, maximum distance from bivouac, and velocity of advance of swarm raids (the data for swarm and fan area are given in combination, because a reliable distinction between these formations is not possible in each case)

Night	Raid	Time (h)	Depth (m)	Width (m)	Area (m^2)	Distance bivouacforefront (m)	Velocity of advance ($cm \cdot min^{-1}$)
4	1	0200	?	?	?	49.0	12.3
7	1	2200	13.5	6.0	53	13.5	9.0
	2	0100	7.3	3.2	16	7.3	?
	3	0300	11.0	3.1	25	11.0	?
8	1	0000	13.5	5.7	42	13.5	5.1
	2	0600	9.0	6.6	30	24.0	11.7
9	1	2320	15.5	9.8	58		8.2
	1	0250	9.0	10.5	54	34.0	8.8
10	1	2200	15.5	5.0	46		13.0
	1	2330	8.7	8.0	>29		4.4
	1	0100	8.7	8.0	>45	30.4	8.2
	1	0230	4.6	6.0	>16		5.3
14	1	2315	9.9	5.2	28	10.9	5.2
	2	0300	7.8	6.8	28		11.7
	2	0550	6.0	7.1	28	32.5	8.8
17	1	2310	10.1	6.2	35		4.8
	1	0150	9.0	8.0	40	33.0	14.3
18	2	0000	12.5	7.3	48	20.5	11.4
			$n=16$ $\tilde{x}=9.5$	$n=17$ $\tilde{x}=6.8$	$n=14$ $\tilde{x}=37.5$	$n=12$ $\tilde{x}=22.25$	$n=16$ $\tilde{x}=8.8$

Predatory behavior

When a worker got in contact with prey, it was able to recruit hundreds of nestmates within a few minutes, and a mass attack followed. Victims were bitten and stung. Soon the prey's movements weakened; the prey was pinned down, torn apart by oppositely pulling groups of workers, and subsequently slowly divided into small pieces that were carried back to the bivouac. Legs and wings of even small prey were cut off. Usually the prey was cut into pieces that could be carried by one forager; larger prey pieces were rarely carried cooperatively.

Discussion

The ecotype "army ant" is characterized by typical behavioral patterns:

1. Army ants form large colonies consisting of many thousands of workers but usually only a single queen.

2. Army ants change their nest sites frequently. Their temporary nests (bivouacs) are modified only slightly. Sometimes the species do not perform any nest building activities at all.

3. Army ants are mass-raiding predators. The exodus begins before prey is localized by scout ants. All foraging activities, i.e., search, attack, and retrieval, are conducted collectively. A new trail system is developed in each raid. The raiding groups are connected to the bivouac by at least one continuous column. The raids are coordinated by communication, based on mass recruitment (Chadab and Rettenmeyer 1975; Topoff et al. 1980).

Besides the Ecitoninae and Dorylinae, which possess all of these characteristics, there are other ants that possess only some of them. Frequent nest relocations seem to be more common in ants than hitherto reported (Smallwood and Culver 1979; Smallwood 1982; Tsuji 1987), particularly in ant species with unspecific nesting demands, like *Monomorium pharaonis* (Wilson 1971), and in species living in unstable habitats such as the leaf litter stratum. Because of the high air humidity at the ground layer of tropical rainforests, nesting in this environment is possible even in unsheltered sites, as frequently observed in bivouac-nesting species. In this habitat, even obligatorily migrating ants can be found that are not migrating hunters like the army ants but true "nomads", e.g., *Dolichoderus cuspidatus* (Maschwitz and Hänel 1985).

Leptanilla was considered to be an army ant because its apterous queens are highly physogastric from time to time. Because of the small colony size in this genus, the term army ant should not be applied to *Leptanilla*. Masuko (1987) gives a convincing explanation for the brood synchronization in *L. japonica*.

The term "army ant", as was introduced by Wilson (1958), includes a number of ant species that live in temporary nests and attack and retrieve the prey co-operatively, e.g., *Leptogenys diminuta*. In this species, however, scout ants search for food solitarily and recruit a group of workers from the nest to the place where prey has been localized. The raiding workers form a distinct group that is not connected to the bivouac by a continuous column of workers (Attygalle et al. 1988). Since the search for food is done solitarily, the foraging behavior of *L. diminuta* differs from the hunting strategy of real army ants in an important feature (Fletcher 1973).

Leptogenys sp. 1 performs the typical army ant behavior patterns:

1. The monogynous colonies consist of several ten thousands of individuals.

2. The raids of *Leptogenys* sp. 1 are coordinated interactions of many thousands of workers that are not directed to specific food sources by successful scouts.

3. The colonies stay in the same site for only a few days. The ants do not build a fixed nest and modify the substrate only very little to a low extent.

Ant species like *Leptogenys* sp. 1 that do not spend much energy on nest building activities may abandon their nest sites frequently. However, for monogynous species nest relocations are linked with the risk of losing the single reproductive female, and the energy costs for emigrations are high for large colonies (Smallwood 1982). The frequent nest relocations in army ants are considered to be advantageous because the colonies are often migrating to new feeding sites (Schneirla 1971; Wilson 1971). Topoff and Mirenda (1980) demonstrated that the food supply may even have a direct influence on the emigration frequency of army ants.

Franks and Fletcher (1983) analyzed the emigration behavior in *Eciton burchelli*. They demonstrated that similar to *Leptogenys* sp. 1, the choice of a new bivouac site is not made at random. The emigrating *Eciton burchelli* colonies follow a certain geometrical pattern that increases the amount of unraided foraging area.

In *Leptogenys* sp. 1 the emigration distances are similar to the raid distances. Since we never observed that the colonies returned to their previous nest site, we can conclude that a considerable shift of their trophophoric field is achieved by the nest relocations. The migratory behavior presumably prevents the area close to the nest site from food depletion.

In spite of the similarities there also are differences between the behavior of *Leptogenys* sp. 1 and the lifestyle of the ecitonine and doryline swarm raiders. Synchronized broods and correlated regular changes between migratory and statary phases, which are lacking in *Leptogenys* sp. 1, are often considered to be typical for army ants. But we have to point out that the brood cycle of some ecitonine species is not as regular as in *Eciton burchelli* and *E. hamatum* (Rettenmeyer 1963). The ecitonine swarm raider *Labidus praedator* sometimes has nonsynchronous broods, and several bivouacs of this species were observed in the same site for months (Rettenmeyer 1963). Also in African driver ants (*Dorylus (Anomma)* spp.), emigrations are irregular (Raignier and van Boven 1955) and not correlated to the brood condition (Gotwald 1978).

The colony size of *Leptogenys* sp. 1 is large, but does not reach the numbers of several hundred thousands or more workers that are attained in species of the Ecitoninae and the Dorylinae (Wilson 1971).

The queen is primarily wingless in all army ants as well as in *Leptogenys* sp. 1. The morphological differences between the workers and the queen are not very pronounced in *Leptogenys* sp. 1, whereas in the colonies of Dorylinae and Ecitoninae, these differences between the workers and the dichthadiiform queens, which have a huge gaster, are enormous. Workers that guard the queen during emigrations (Schneirla 1971) are not found in *Leptogenys* sp. 1. While the workers of most ecitonine and doryline species are polymorphic, *Leptogenys* sp. 1 workers are monomorphic. A narrow range of size is also found in the dorylines of the genus *Aenictus* (Schneirla and Reyes 1966).

Recent field studies (Franks 1982; Franks and Fletcher 1983) and the data collected by Willis (1967) permit a comparison between the *E. burchelli* average swarm raid and the average foray in *Leptogenys* sp. 1. The raid of *Leptogenys* sp. 1 attains a similar width, but is much shorter and advances much slower than the foray of *E. burchelli*. The swarm raid of this ponerine ant species contains only about one-fifth of the workers that may be involved in the raids of *E. burchelli*.

Whereas *E. burchelli* colonies generally produce one swarm per day, the colonies of *Leptogenys* sp. 1 often conduct two or more raids each night. The nightly raids of a colony of *Leptogenys* sp. 1 cover an area of approximately half the size of the daily foraging area of *E. burchelli.*

Comparison with other Leptogenys species

We began our studies on this genus with *Leptogenys processionalis* (*L. ocellifera*) from Sri Lanka (Maschwitz and Mühlenberg 1973, 1975). This species as well has many army-ant-like habits, but also some distinct specialized characteristics. The colony size is similar to that of *Leptogenys* sp. 1. The ants may change their nest frequently; however one colony was observed at the same site for at least ten weeks. In contrast to the characterization of army ant behavior already mentioned, the raiding ants leave the temporary nest to deepened trunk trails that may be used for several weeks.

In the area where our studies on *Leptogenys* sp. 1 were conducted, we found a total of twelve *Leptogenys* species, five of which have army ant characteristics. Besides *Leptogenys* sp. 1, these species are *L. mutabilis, L. birmana, L. crassicornis,* and *Leptogenys* sp. 2 (unidentified and possibly undescribed species resembling *L. borneensis*). Though we have not yet finished our studies on the behavior of these species, differences in their ecology are obvious. *L. mutabilis* is an epigaeic mass raider, but contrary to *Leptogenys* sp. 1, the workers forage mainly beneath the leaf litter. *L. crassicornis* is hypogaeic, but parts of the raid columns of this small species sometimes were discovered above ground, at night.

The seven species that are not army ants in the sense already mentioned search for prey solitarily. After encountering the prey, they either recruit a group of nestmates, e.g., *L. diminuta,* or even attack and retrieve their prey solitarily, e.g., *L. peuqueti.*

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Note added in proof:

Kistner (Chico, Calif.) is describing the two Zyrasini species as *Maschwitzia ulrichi* and *Togpelenys gigantea* (new species and new genera) (in preparation).